

SOME EVOLUTIONARY TRENDS IN THE BAMBUSOIDEAE (POACEAE)¹

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ABSTRACT

Bamboos, which have woody culms, and several genera with herbaceous culms share a similar type of leaf anatomy and epidermis. Various other morphological features, including a distinctive type of seedling, also indicate a close relationship that supports the grouping of these genera together into a single subfamily, the Bambusoideae. A review of the chromosome numbers in the subfamily reveals that the herbaceous members are mostly diploid while the woody ones are polyploid, with $x = 12$ the basic number. Such evidence corroborates the hypothesis that bamboos have been derived from herbaceous ancestors. Most bamboos flower infrequently and have had far less opportunity for floral evolution than have the herbaceous members, which flower continuously or at least seasonally. The most primitive inflorescences have therefore been retained in the bamboos while highly specialized ones have developed in the herbaceous members. A knowledge of the former type of inflorescence is useful in an interpretation of the latter. With this in mind, the inflorescence of the herbaceous bambusoid grass, *Streptochaeta*, has been reexamined. This genus has long been considered to be the most primitive grass, in great part due to the presence of three large structures in the spikelet, thought to be primitive lodicules and two structures interpreted as a primitive, two-parted palea. Comparison of *Streptochaeta* with other members of the Bambusoideae suggests that the spikelet in fact lacks both lodicules and palea and that these structures represent instead bracts on different axes of a highly modified pseudospikelet. Such a pseudospikelet is comparable to that of a bamboo. While *Streptochaeta* may be considered primitive in its herbaceous nature and possession of a pseudospikelet, it must be regarded as advanced in other features, among them the lack of lodicules. No one member of the subfamily can be considered most primitive. The least advanced inflorescences are retained in bamboos, such as *Bambusa*, while the most primitive growth form occurs in herbaceous genera like *Streptochaeta*, *Streptogyna*, and *Pharus*. The significant trends of evolution within the subfamily become apparent, however, only when all of the genera—woody and herbaceous—are considered together. The bambusoid line—with its complex leaf anatomy and epidermis—is itself specialized and not to be regarded as the precursor of the other groups of grasses.

The major, large, natural groups of grasses can be determined by relatively few factors that are of basic importance in the family, among them the internal structure of the leaf and features of the leaf epidermis and embryo. Other characters, such as chromosome number and seedling type, in correlation with these result in the recognition of six or seven major groups that most agrostologists agree upon as being natural. These are commonly known as the arundinoid (phragmitoid), bambusoid, centostecoid, chloridoid (eragrostoid), oryzoid, panicoid, and pooid (festucoid). Often these groups are called subfamilies. Odd genera here and there have sometimes been considered of equal importance so that in the literature we find whole subfamilies based upon single genera: Anomochlooideae and Micrairoideae are examples.

The bambusoid group is best known by its Gargantuan members, the tree grasses, such as *Dendrocalamus giganteus* of northern Burma, whose culms may

¹ The illustrations, except for Fig. 7, were prepared by Alice R. Tangerini, to whom I am indeed indebted for her skillful rendition of a multitude of new and often difficult structures. Figure 7 was drawn by Mrs. Gesina Berendina Threlkeld as part of a series of illustrations of Ceylonese bamboos, to be published as a unit at a later date.

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reach 30–35 m in height and 25–30 cm in diameter. The clumps of such bamboos reach enormous proportions and the plants are known for their propensity to continue growing vegetatively, even for decades, before they flower. Size, complexity of body, and rarity of flowering have contributed to the neglect that bamboos have received from systematists and the taxonomic confusion that has long plagued them. Not all bamboos, however, are so large as *Dendrocalamus*. At the other end of the scale we find *Arundinaria pygmaea*, whose wiry culms reach no more than half a meter in height, but like the bigger members also branch at the nodes and flower seldom.

Regardless of size, both *Dendrocalamus* and *Arundinaria* share a number of features that are common throughout the bamboos: a specific type of leaf anatomy and epidermis; distinctive seedling; flowers with three lodicules, often six stamens, and three stigmas; and fruit with a small embryo and linear hilum. Many other grasses of small stature that inhabit shaded forests also possess these basic features, which demonstrate a natural relationship. Besides their smaller stature, they do not have such complex branching as the bamboos nor such long-lived culms, and they commonly flower throughout the year or at least seasonally. These grasses, with the bamboos, constitute the subfamily Bambusoideae.

We refer to the one group of Bambusoideae as “herbaceous bambusoid grasses” and to the other as “woody bambusoid grasses,” or simply bamboos. When we speak of “woody,” we mean this in the sense of being hard, not like the stem of a dicotyledonous tree that produces secondary xylem. The bamboo culm is characterized by collateral bundles embedded in parenchymatous tissue, with the bundles toward the inside more separated from one another than those toward the periphery, which are smaller and occur very close together. A cap of fiber strands usually occurs on both sides of the bundle, and this abundant sclerenchyma in the culm, along with thick-walled and lignified ground tissue, accounts for the hardness of the culm. Some additional strengthening may be contributed by the silica that is present in the epidermis. Detailed studies on the anatomy of the bamboo culm have been carried out by Grosser and collaborators (Grosser, 1970; Grosser & Liese, 1971; Grosser & Zamuco, 1971).

All bambusoid grasses grow in association with woody vegetation and are never components of prairies or grasslands, being most common in temperate woodlands or tropical forests or, if herbaceous, in the shaded understory of warm forests. They are usually dependent on humidity, at least during the growing season; those few that grow in drier regions or areas with a dry season may lose their leaves during this period. Bambusoid grasses are most abundant in the world's tropics and subtropics, but a few members are found in temperate-cold areas of both hemispheres. They occur between 46° north latitude and 47° south latitude and from sea level to as high as 4,000 m elevation, and are found on all continents except Europe. The bambusoid grasses represent the most widespread and diverse assemblage of genera and species within the family. So distinctive and natural is the group that Tzvelev (1976), in his recent system of classification of grasses, recognized it as one of his two subfamilies, the other being the Pooideae. Following are some of the basic characteristics of the Bambusoideae, a more detailed elaboration of which is given in Calderón & Soderstrom (1980).

BAMBUSOIDEAE

General morphology: perennials, herbaceous or woody, rhizomatous; culms when woody branched at the nodes; leaf blades usually flat, broad, lanceolate or linear-lanceolate, articulate with the sheath by a petiole that orients the blade in different positions; blades with tessellate venation strongly or weakly manifest; flowering seasonal or occurring infrequently; inflorescences of different types, often of complex systems of partial inflorescences of limited branching or unlimited branching and production of spikelets or pseudospikelets; spikelets or pseudospikelets 1-many-flowered, without glumes or with 1-several "transitional" glumes; lemmae 3-many-nerved, awnless or only seldom awned and then the awn not geniculate; palea 2-many-nerved, keeled or rounded dorsally, exceptionally bifid; lodicules generally 3 (0-6, rarely many), usually large and with hairs of different types and well-developed vascularization; stamens 3-6 (rarely 2, occasionally many), sometimes partially fused or monadelphous; stigmas 2 or 3; fruit usually a caryopsis, sometimes an achene or fleshy; hilum linear, almost as long as the fruit; embryo small in comparison to the fruit.

Seedling: coleoptile usually short and not elevated from the caryopsis; first one to several leaves usually bladeless or with a reduced blade; first expanded blade usually broad, ovate or lanceolate, horizontal in position.

Leaf anatomy: leaf blade with a conspicuous midrib containing a complex vascular system of several bundles in 2 rows, strongly developed sclerenchyma and ground tissue; mesophyll with cells arranged in horizontal layers parallel to the epidermis, not radiate; chlorenchyma composed of arm cells and translucent fusoid cells at each side of the vascular bundle and in between layers of arm cells; bundle sheaths always double and well developed, the outer sheath with very few chloroplasts; transverse veinlets connecting the longitudinal vascular bundles.

Leaf epidermis: with short cells in pairs or sometimes in rows over the veins; silica bodies usually cross shaped, saddle shaped, of olyroid type or of intermediate forms; microhairs nearly always present, bicellular with both cells of about the same length and with a rounded apex, or sometimes of 3 or 4 cells, papillae common and abundant on the long cells and overarching the stomata; long cells with thick, sinuous walls; stomata usually with low dome-shaped or sometimes triangular subsidiary cells.

The herbaceous bambusoid grasses, which are fewer in number than bamboos but have received more attention in recent years, are more clearly understood than the bamboos. We are able to delimit the genera of herbaceous bambusoid grasses and are able to recognize related groups of genera, or tribes. While this is also true for some bamboos, for the most part generic limits are still poorly understood and consequently tribes are not yet recognized for most.

We presently recognize eight tribes of herbaceous bambusoid grasses, the following six occurring in the American tropics: Anomochloae, Olyreae, Parianeae, Phareae, Streptochaetaeae, and Streptogyneae. Only two of these are represented outside of the Americas. The Phareae contains two genera, *Pharus* of the American tropics and *Leptaspis* of the Old World tropics, and the Streptogyneae is monotypic, with one species of *Streptogyne* occurring in the New

World and one species in Africa, southern India and Ceylon. The other American tribes vary in size, with the Anomochloae and Streptochaeteae each monotypic (*Anomochloa* and *Streptochaeta*), the Parianeae with two genera (*Eremitis*, *Pariana*), and Olyreae with 15 (*Arberella*, *Cryptochloa*, *Diandrolyra*, *Ekmanochloa*, *Froesiochloa*, *Lithachne*, *Maclurolyra*, *Mniochloa*, *Olyra*, *Piresia*, *Raddia*, *Raddiella*, *Rehia*, *Reitzia*, *Strephium*). A key to the herbaceous American tribes appears in Calderón & Soderstrom (1980).

The tribe Atractocarpeae is represented only in Africa, and contains the genera *Guaduella* and *Puelia*, while the monotypic tribe Buergersiochloae is known only from the genus *Buergersiochloa* in New Guinea. The herbaceous bambusoid grasses are most abundant in the New World where they reach their greatest diversification and comprise well over one hundred species, many still undescribed.

There are 17 described genera of bamboos in the New World alone, of which only two occur in Asia, *Arundinaria* and *Bambusa*. The others are all endemic to the American continent. An equal or greater number of bamboo genera occur in the Old World, with many endemic to Madagascar, surpassing the number that occur in all of Africa.

The trends of evolution in the subfamily become apparent only when we study all the genera together, herbaceous and woody. Previous systems of classification have often obscured these patterns, for the woody genera were placed in a single tribe, Bambuseae, and the herbaceous genera were scattered in widely unrelated tribes, such as the Hordeae and Paniceae, that pertain to other subfamilies.

A survey of many bambusoid seedlings shows that they are of a unique type, with certain features not found in the seedlings of other grasses. The fact that the seedlings of both herbaceous and woody members are similar strengthens the argument that these genera are closely related, which corroborates the conclusions based on studies of the leaf anatomy and epidermis.

The development of the woody habit and emphasis on vegetative reproduction in the bamboos has been accompanied by a decrease in flowering. Most bamboos bloom only at long intervals, these sometimes as much as 120 years. This has in effect prevented gene interchange in bamboos and arrested evolution of the inflorescence. On the other hand the herbaceous members, which bloom throughout the year or at least seasonally, in comparison with the bamboos have had countless generations of flowers and continuous opportunity for evolution of the flowering system. Among the herbaceous members, we therefore encounter highly specialized inflorescences and spikelets while in the bamboos we find them to be more primitive and less specialized.

The herbaceous bambusoid genus, *Streptochaeta*, long considered to be the most primitive of all grasses, can now be reinterpreted in light of the above ideas. A study of its seedlings confirms that the genus is bambusoid. A knowledge of chromosome numbers in the subfamilies suggests that the somatic number of $2n = 22$ in this genus represents a diploid based on a derived basic number. Analysis of the so-called spikelet of the genus and comparison of it with the inflorescence of a primitive bamboo reveals that the flowering unit is in fact a highly modified pseudospikelet.

While *Streptochaeta* does indeed have primitive features, our study of other

bambusoid seedlings and chromosomes shows that two other genera must also be primitive. These genera, *Streptogyna* and *Pharus*, have peculiar, apparently undifferentiated, seedlings, and are diploids, based on the primitive number of $x = 12$. Their present-day distribution also points to an archaic existence, for one species of *Streptogyna* occurs in the New World and one in the Old World. *Pharus* is represented in the New World by several species and its sister genus, *Leptaspis*, is represented by several species in the Old World.

The herbaceous bambusoid genus, *Puelia*, which is endemic to Africa, also is a diploid based on $x = 12$. We thus find a concentration of primitive herbaceous types in present-day tropical Africa, with the most highly specialized herbaceous genera in the New World. The polyploid bamboos, which are apparently derived from herbaceous ancestors, occur in the Old and New World alike. The highest polyploid bamboos, however, are found in Asia.

THE BAMBUSOID SEEDLING (Figs. 1–3)

Studies of the embryo in grasses have been so numerous and interpretations of the component structures so diverse that a voluminous literature exists. The reader is referred to Brown (1960), who reviewed the major papers and interpretations of each author. I do not, however, agree with the conclusions that he personally drew. His paper was followed in close sequence by at least two others that do not agree with his findings either: these are Guignard (1961) and Negbi & Koller (1962).

The grass embryo is of special interest because it has unique structures whose homologies have been the subject of much debate. Most studies have been made on cultivated grasses such as wheat (*Triticum*) and maize (*Zea*), an unfortunate situation as these grasses have been so modified by man. I agree with Reeder (1953) who felt that more primitive grasses should be used for study of these structures; he himself chose one, *Streptochaeta*, for his study of the coleoptile.

The grass embryo, together with the endosperm, and surrounding wall structures comprise the grass fruit, which is generally a caryopsis. In rare, specialized cases, such as the bamboo genus *Melocanna* (Stapf, 1904), the endosperm is lacking in the mature fruit and the pericarp, along with the scutellum, becomes fleshy.

We can imagine the grass plant in its earliest stages as an axis, the basic part being the embryonal axis with the main seat of differentiation the node where the scutellum is attached. We may call this the first node of the grass plant and it occurs within the embryo. The axis continues upward and the next node marks the origin of the coleoptile. These two nodes and the internode between them are important in our discussion as these structures are unique to grasses and not really comparable to embryos of other monocotyledons.

The scutellum is a flat organ that is specialized for absorption of nutrients from the food reserve or endosperm. It remains within the fruit as the other parts become visible at germination. Opposite the scutellum there is sometimes present, as a nonvascularized outgrowth, a structure called the epiblast. The coleoptile is a sheathing structure and is generally closed; it protects the growing apex of the embryo, which it completely encloses. At germination the growing apex, or plumule, pushes through it.

Below the point of attachment of the scutellum is an elongated zone of tissue, the radicle, enclosed in a sheathing structure called the coleorhiza. The coleorhiza terminates in suspensor cells.

The scutellum is generally accepted to be a cotyledon. For this reason the node where it is attached is called by some the "cotyledonary node," but I prefer the term "scutellar node," as employed by Avery (1930), as it is descriptive rather than interpretive. By the same reasoning Avery's term, "coleoptilar node," for the next node is appropriate. According to some authors (Negbi & Koller, 1962), the epiblast represents a second cotyledon. However, it may be nothing more than an outgrowth of the coleorhiza and, furthermore, it is not always present.

For practical purposes, since a scutellum and coleoptile are always present, let us use them as markers of the first and second nodes of the embryonal axis, the region in between being the first internode of the plant's axis as accepted by Avery. This internode is somewhat specialized, as we might expect, and each succeeding internode becomes anatomically more like those of the culm. Since the time of Čelakovský (1897), this region has often been referred to as the mesocotyl, an interpretive designation that relies on a theory that regards this as an elongated node belonging neither to epicotyl nor hypocotyl.

The plumule, enclosed within the coleoptile, consists of numerous nodes and internodes, the nodes bearing the embryonic leaves. Its axis is a continuation of the embryonal axis; its first internode, the one just above the coleoptile (which is the second internode of the axis), is called a "transition internode" by Avery since it has an anatomical structure intermediate between that of the first internode and the next higher one, the third. Upon germination the plumule elongates and pushes through the coleoptile, which is a closed sheathing structure that is generally two-nerved. The second internode may elongate greatly at this time, elevating the remainder of the plumule. At the same time the radicle elongates and pushes through the coleorhiza. Some authors consider the coleorhiza to be a modified primary root, especially since it terminates in suspensor cells, which are characteristic of that organ. If the coleorhiza is indeed homologous to the primary root, and this seems reasonable to me, the structure normally referred to as "primary root" is an adventitious one. To avoid the use of an interpretive term in identifying this structure that emerges through the coleorhiza, I am using the word "radicle."

The structure of the embryo, its size relative to the endosperm, structure of the starch, and type of seedling have all provided useful characters in grass systematics. The most important papers on this subject, especially the embryo, are those of Yakovlev (1950) and Reeder (1957, 1962).

Numerous publications by Kuwabara, commencing with his 1960 paper in English, have shown the systematic significance of grass seedlings, a topic discussed more recently in detail by Hoshikawa (1969). The latter author studied over 200 grass species in 88 genera and found that, as with embryo types, seedling types could also be used to delimit major natural groupings within the family.

Unfortunately, the terminology of Hoshikawa is not clear and is sometimes misleading. For example, the coleoptilar node (as I am using it) is referred to by him as the "cotyledonary node," a term often used for the first or scutellar node.



FIGURE 1. Seedlings of Bambusoideae.—a. *Aulonemia* aff. *aristulata*, Brazil, Espírito Santo, Linhares, Soderstrom & Sucre 1901.—b. Embryo of *Streptochaeta spicata* just beginning to emerge from fruit, Costa Rica, Puntarenas, Palmar Sur, Pohl & Calderón 10089.—c. *Streptochaeta spicata*, same collection as b.—d. *Lithachne pauciflora*, Puerto Rico, Mayagüez, Soderstrom 1801.—e. Detail of germinating fruit of *Lithachne pauciflora*, same collection as d.—f. *Ochlandra stridula*, Ceylon, near Anandara, Soderstrom 2563.

For the scutellar node he coins the term, "transitional node." In spite of these drawbacks, his scheme is interesting and of value. He points out differences that are quite useful in differentiating seedlings, such as points of origin of adventitious roots and their relative rates of development, and elongation or suppression of the first internode (his "mesocotyl") and second internode.

Based on the study of seedlings of seven bamboo species, Hoshikawa (1969) defined the bambusoid seedling as follows, his terminology following mine in parentheses: the first internode (mesocotyl) does not elongate, adventitious roots are lacking from both the scutellar (transitional) node and coleoptilar (cotyledonary) node, and the blades of the leaves (leaves) from the lowest nodes are entirely suppressed or are only weakly developed.

Unaware of this paper, Calderón and I (1973) defined the bambusoid seedling on the basis of an herbaceous genus, *Maclurolyra*. We stated that the coleoptile is short and not elevated above the caryopsis by an internode (i.e., the first internode does not elongate), the first two to several leaves lack blades or the blades are reduced, and the first expanded blade is broad, ovate-lanceolate, and horizontal in position. We also pointed out the similarity of bambusoid to oryzoid grasses in the presence of reduced blades in the first leaves of the new shoot, but that in the latter group the first expanded blade is linear and ascending rather than horizontal in position.

I have now examined the seedlings of several more herbaceous and woody bamboos, including the genera *Streptochaeta*, *Streptogyna*, and *Pharus*, all of which belong to different tribes and have been considered as archaic and related to bamboos. All of the seedlings were collected from beneath parent plants in the field, with the exception of *Streptogyna*. In that case I collected the fruits in Espírito Santo, Brazil, on 16 March 1972, and planted them in pots at the Jardim Botânico in Rio de Janeiro on April 13. Seedlings were collected at intervals of about one month and preserved in FAA (90 parts of 50 percent EtOH : 5 parts glacial acetic acid : 5 parts formalin).

The following descriptions of the seedlings (whether of herbaceous or woody genera, as indicated) may be compared with the illustrations that appear in Figs. 1-3.

SEEDLING DESCRIPTIONS

1. *Arundinaria gigantea* (Fig. 2f) woody
A short coleoptile is followed by two sheaths and a leaf with a small ovate, more or less horizontal, blade.
2. *Aulonemia* aff. *aristulata* (Fig. 1a) woody
The first and second internodes do not elongate; the coleoptile remains very short, followed by two short sheaths, a longer sheath, and the first leaf with a small, oval horizontal blade.
3. *Diandrolyra* sp. (Fig. 2e) herbaceous
The short coleoptile is followed by two sheaths, and then a leaf with a small, horizontal, ovate blade.
4. *Lithachne pauciflora* (Figs. 1d-e) herbaceous
In one seedling the coleoptile is short, followed by two sheaths, and a leaf with an ovoid-lanceolate blade horizontal in position. In the other seedling an

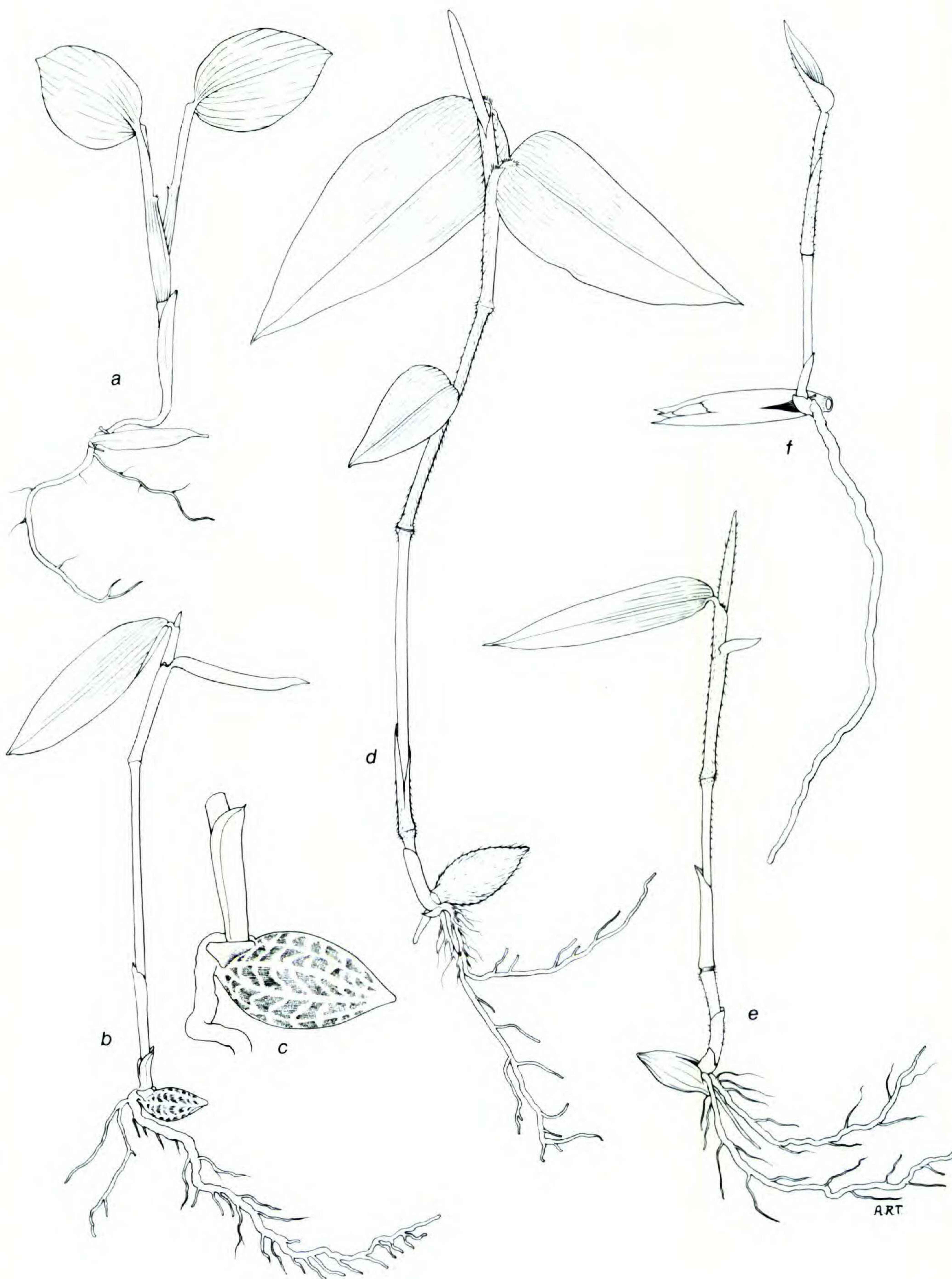


FIGURE 2. Seedlings of Bamusoideae.—a. *Pharus* sp., Brazil, Bahia, Calderón 2171.—b-c. *Raddia* sp., Brazil, Rio de Janeiro, Soderstrom, Sucre, & Calderón 1858.—d. *Olyra loretensis*, Colombia, Leticia, Soderstrom 1429.—e. *Diandrolyra* sp., Brazil, Rio de Janeiro, Soderstrom & Sucre 1935.—f. *Arundinaria gigantea*, USA, Maryland, McClure, bamboo garden introduction no. 2762.

elongated portion precedes a node bearing some roots that pierce the coleoptile that covers it. Here it is the second internode that has elongated. The node bearing the first leaf is covered by the elongated coleoptile.

5. *Ochlandra stridula* (Fig. 1f) woody

The coleoptile is short, followed by two sheaths and then several closely overlapping sheaths, each bearing a small, more or less horizontal-ascending blade. Germination of a bud, apparently in the axil of the coleoptile, gives rise immediately to a second shoot similar to the first. Quick germination of further buds produces a miniature clump of new shoots at the seedling stage.

6. *Olyra loretensis* (Fig. 2d) herbaceous

The short coleoptile is followed by two sheaths without blades; the following leaf bears a small, ovate, more or less horizontally positioned blade.

7. *Pharus* sp. (Fig. 2a) herbaceous

The first internode does not elongate, the second hardly so or sometimes extending for some length, with the coleoptile elongating concomitantly. The third node produces a leaf with expanded blade, which is broad, ovate, and horizontally positioned, but without reduced blades preceding it.

8. *Raddia* sp. (Figs. 2b-c) herbaceous

The short coleoptile is followed by one leaf with a tiny erect blade and a second one with the first expanded blade, which is broad-lanceolate and horizontal.

9. *Streptochaeta spicata* (Figs. 1b-c) herbaceous

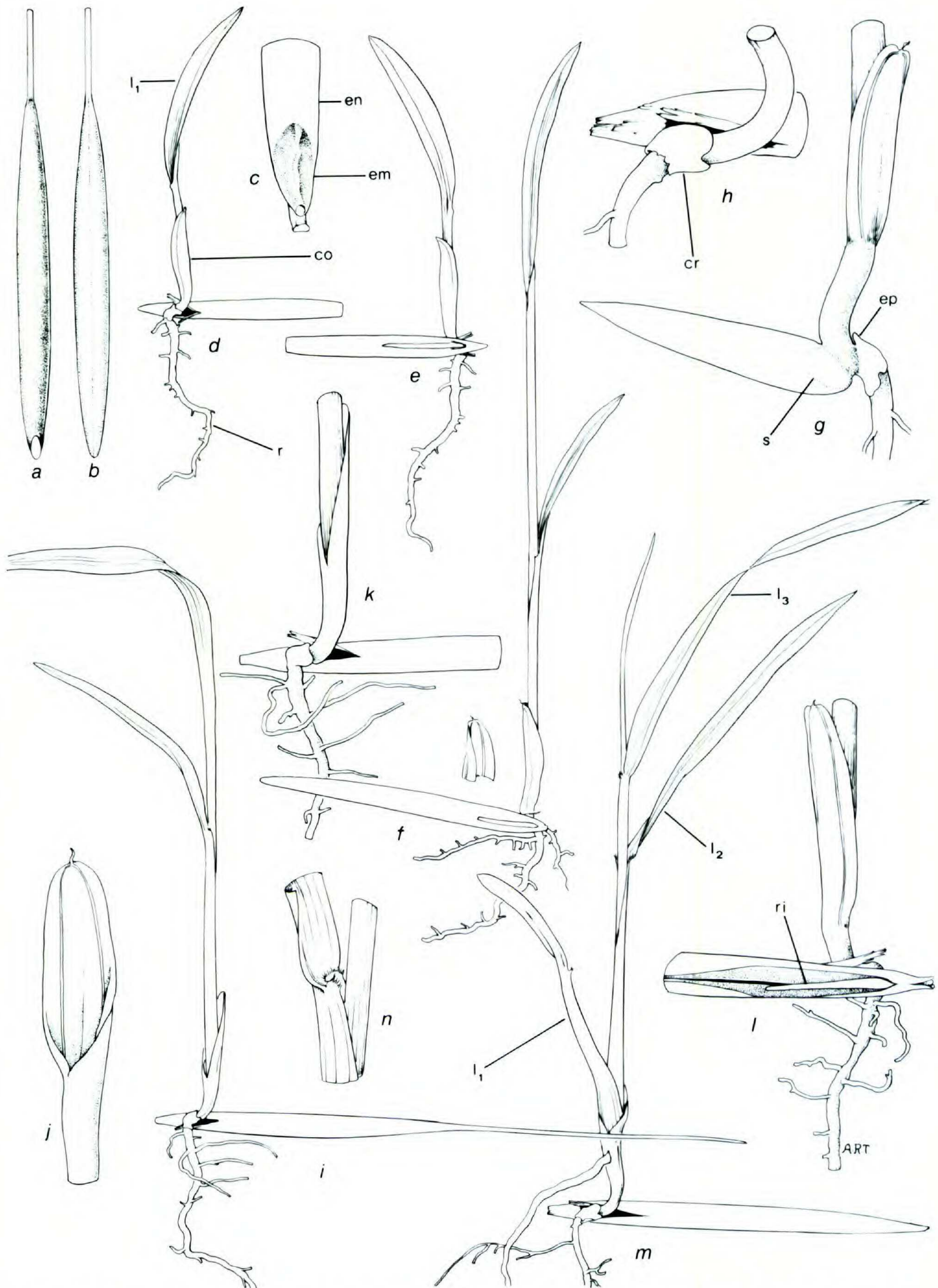
The first internode does not elongate; the second internode is very short. There are up to three leaves without blades or with reduced blades that precede the first leaf with an expanded one, which is broad and horizontally positioned. The short coleoptile is 5-nerved.

10. *Streptogyna americana* (Figs. 3a-n) herbaceous

The first internode does not elongate; the second internode elongates, as does the coleoptile. The third node produces a root and leaf with narrow, ascending, fully developed blade. There are no reduced blades nor is the first blade broad and horizontal. The basal portion of the coleoptile is thickened and appears to be fused to the second internode but careful dissection reveals them to be free from one another. There are two strong nerves in the coleoptile and sometimes a faint line that appears to be a median nerve, although this may only be an artifact. However, the coleoptile is mucronate, a condition not found in any of the other bambusoid grasses I have studied.

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FIGURE 3. Fruit and seedling of *Streptogyna americana*.—a. Caryopsis showing relation of embryo (at base) to endosperm.—b. Caryopsis showing long linear hilum.—c. Base of caryopsis enlarged to show embryo.—d. Seedling 5–6 weeks old breaking through covering bracts, showing coleoptile (co), radicle (r), and first leaf (l_1).—e. Opposite side of d showing seedling in relation to the persistent rachilla internode.—f. Seedling 8 weeks old.—g. Detail of f at region of embryo emergence, showing the coleoptile, epiblast (ep), coleorhiza, radicle, and scutellum (s), covered by the pericarp.—h. Enlargement of g showing coleorhiza (cr).—i. Seedling 3 months old. The mature elongated style is shown here, but broken off or shortened in the other drawings.—j. Upper part of coleoptile of f. ($\times 6$).—k. Detail of i at region of embryo emergence.—l. Detail of i at region of embryo emergence, from side of persistent rachilla internode (ri).—m. Seedling 4 months old showing 3 developed leaves.—n. Ligule of first leaf of f. [Drawings a and b based on *Swallen 5089* from Obidos, Pará,



Brazil. The seedlings are all taken from plants cultivated at the Jardim Botânico, Rio de Janeiro, Brazil, from fruits collected by *Soderstrom & Sucre 1906* in Brazil, Espírito Santo, Reserva Florestal de Linhares, 16 March 1972. All fruits were planted 13 April 1972: *d* was removed at the end of May, *f* on June 14, *i* on July 16, and *m* on August 16.]

BAMBUSOID SEEDLING DEFINED

On the basis of published findings and the additional seedlings described here, we can make the following definition of the bambusoid seedling:

The first internode does not elongate; the second internode is usually short with the coleoptile remaining short, but occasionally it elongates with the coleoptile elongating as well; the first node or first several above the coleoptilar node bear leaves that lack a blade or the blade is reduced; the first expanded blade is usually broad, ovate-lanceolate and positioned horizontally; adventitious roots are usually lacking but may occur at both the scutellar and coleoptilar nodes; a bud may be produced at the coleoptilar node.

While this is a generalized description, we find that the seedlings of two genera in our study depart from this. *Pharus* and *Streptogyna* both lack reduced blades; in the former the first blade is expanded, large and ovate, and in the latter it is narrow and ascending.

The principal features of bambusoid grass seedlings then are the nonelongation of the first internode and general lack of roots at the scutellar and coleoptilar nodes. In the oryzoid and pooid grasses, for example, there is an elongation of the first internode and production of roots at the coleoptilar node.

CHROMOSOMES (Fig. 4)

Chromosome counts in the Bambusoideae are by no means numerous, yet there is a sufficient number to allow us to discern some general patterns and form some postulations. The following account is based on data from the literature and from counts made on plants that we have collected in the field or have in cultivation. In each case I am citing the single reference for the count, or a representative one when there are more.

The differences in somatic numbers in the Bambusoideae are great, ranging from $2n = 14$ in *Olyra fasciculata* (Morisset, in litt.) to $2n = 72$ in *Dendrocalamus giganteus* (Gould & Soderstrom, 1974). That the former is an herbaceous member and the latter a gigantic woody one is particularly interesting as, in general, the lower, diploid numbers are found in the herbaceous genera and higher, polyploid numbers in the woody.

A basic number of $x = 12$ is found in a few of the herbaceous bamboos and the tetraploid complement, $2n = 48$, among many of the woody bamboos. In diploid form, $2n = 24$, this number occurs in genera of three tribes of herbaceous bambusoid grasses: *Streptogyna* (Kammacher et al., 1973) of the Streptogyneae; *Leptaspis* (Tateoka, 1958) and *Pharus* (Pohl & Davidse, 1971) of the Phareae; and *Puelia* (Dujardin, 1978) of the Atractocarpeae. Hsu (1972) gave this number for two woody bamboos from Taiwan, *Bambusa oldhamii* and *B. stenostachya*.

The tetraploid number of $2n = 48$ occurs throughout the bamboos in widely unrelated taxa, such as *Arundinaria gigantea* (Gould, 1960) from the United States, *Neurolepis* (Gould & Soderstrom, 1970) from Andean South America, *Chimonobambusa* (Mehra & Kalia, 1976) from the Himalayas, *Indocalamus* (Janaki Ammal, 1945) of Ceylon, and *Shibataea* (Okamura & Kondo, 1963) from Japan.

Hexaploids of $2n = 72$ have been recorded for several woody bamboos, especially those largest in stature, including *Oxytenanthera abyssinica* (Reeder &

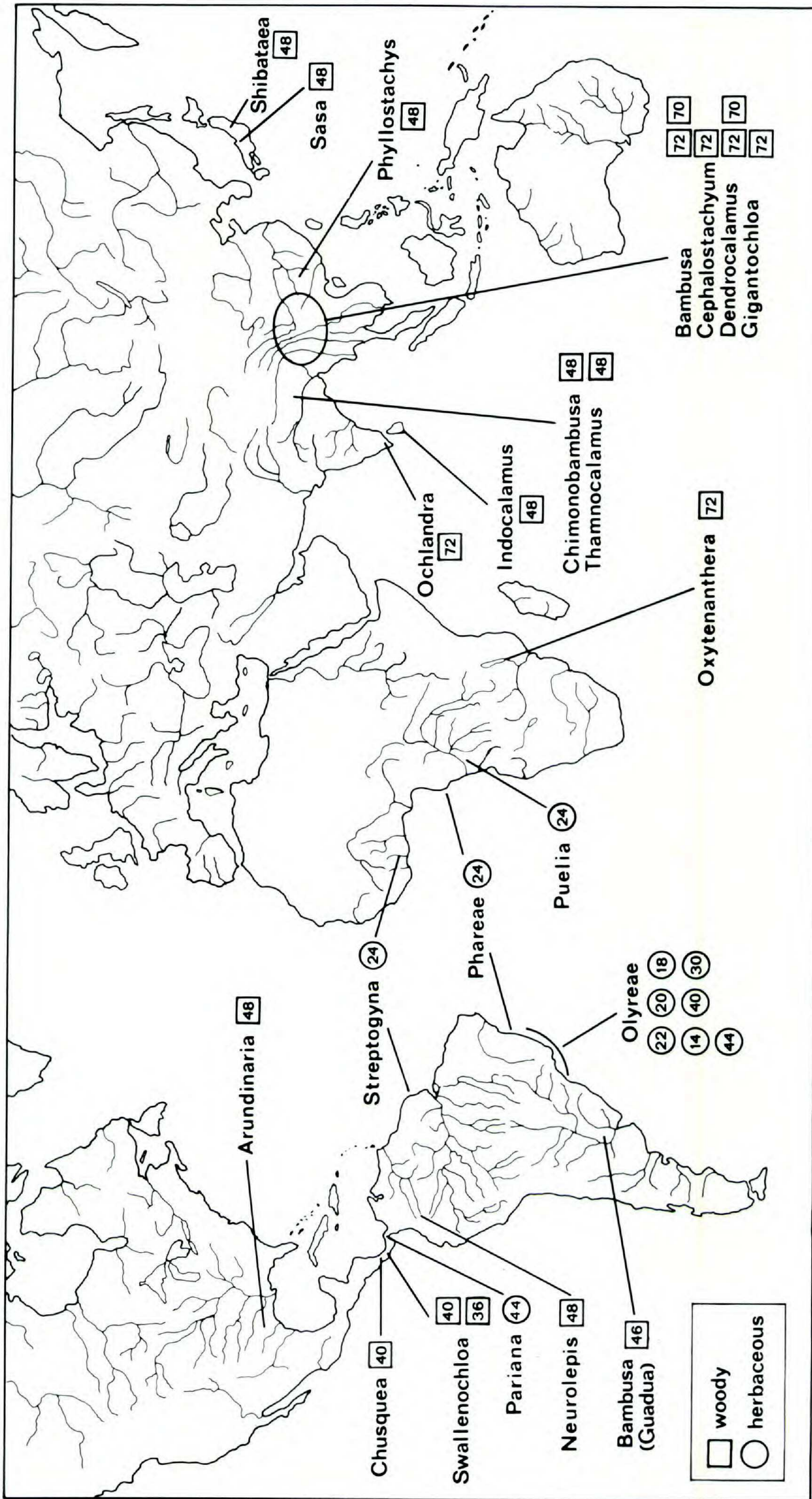


FIGURE 4. Chromosome numbers (2n) in the Bambusoideae.

Singh, 1967) of Africa and *Ochlandra* (Janaki Ammal, 1945) from India. However, there is a noticeable concentration of hexaploids in the mountains of northern Burma and western China. The hexaploid bamboos that are native to this region include *Bambusa polymorpha* (Janaki Ammal, 1945), *B. tulda* (Christopher & Abraham, 1971), *Cephalostachyum pergracile* (Sarkar et al., 1977a), *Dendrocalamus brandisii* (Janaki Ammal, 1945), *D. giganteus*, *D. hamiltonii* (Mehra & Sharma, 1972), *D. longispathus* (Janaki Ammal, 1945), *D. strictus* (Richarria & Kotval, 1940), and *Gigantochloa macrostachya* (Sarkar et al., 1977b). The hexaploid bamboos from this region include the largest species, *Dendrocalamus giganteus*, and some of the most widely planted and economically important, such as *Bambusa tulda* and *B. polymorpha*.

It is interesting to point out that Janaki Ammal (1950, 1954) found this region to contain the highest polyploid races of *Rhododendron* and *Buddleia*. Darlington (1973) speaks of this region, between the headwaters of the Yangtze and Salween rivers, as the most diversified and florally richest in the world. He feels that in colonizing new habitats in this territory new polyploid races and species are produced and survive in abundance. He regards this as a special situation in which extreme or peripheral ecological conditions confront the species in what is geographically the interior of its range.

In the New World we encounter interesting divergences from the pattern in the Old World. For example, the species of *Guadua*, now regarded as a subgenus of *Bambusa*, have a somatic number of $2n = 46$. This number has been found in three species of the subgenus so far examined: *B. capitata* (Gould & Soderstrom, 1967), *B. chacoensis* (Quarín, 1977), and *B. paraguayana* (Quarín, 1977).

We find divergences in the counts for the American bamboo genera, *Chusquea* and *Swallenochloa*. The expected tetraploid number of $2n = 48$ was given by Janaki Ammal (1959) for the species of *Chusquea* that she studied, while Pohl & Davidse (1971) found $2n = 40$ for the species of *Chusquea* and *Swallenochloa* that they examined. An even lower number, $2n = 36$, was reported by Virkki (1963).

The greatest variation of somatic numbers within a group occurs in the tribe Olyreae, which contains 15 described genera of herbaceous bambusoid grasses. The tribe is endemic to tropical America except for the single weedy species, *Olyra latifolia*, which has become naturalized elsewhere. Somatic numbers of 22 and 20 are the most common in the tribe, but 18 and 14 have also been reported, as well as 30, 40, and 44. A basic number of $x = 12$ has not been found in any member of this tribe.

In the genus *Olyra* itself we find $n = 11$ to be common: in *O. latifolia* we have diploids of $2n = 22$ (Davidse & Pohl, 1972a) and tetraploids of $2n = 44$ (Davidse & Pohl, 1974), while in another widespread weedy species, *O. micrantha*, we have only $2n = 40$ (Gould & Soderstrom, 1967). *Olyra taquara* is a diploid, with $2n = 20$, and *O. fasciculata* a diploid with $2n = 14$ (Gould & Soderstrom, 1967).

Other genera in the tribe include *Cryptochloa*, with a report of $2n = 22$ for *C. concinna* (Davidse & Pohl, 1974) and $2n = 20$ for an undescribed species (Soderstrom 1380) from Colombia (Gould in litt.). Other olyroid genera with a basic number of $n = 11$ are *Lithachne*, where both the diploid, $2n = 22$ (Pohl

& Davidse, 1971), and tetraploid, $2n = 44$ (Quarín, 1977), have been found; *Mac-lurolyra tecta*, $2n = 22$ (Calderón & Soderstrom, 1973); and *Piresia*, $2n = 22$ (Gould & Soderstrom, 1967). A basic number of 10 has been found in *Raddiella esenbeckii* (as *R. nana*) by Davidse & Pohl (1972b) and *Rehia* (as *Bulbulus*) *nervata* by Gould & Soderstrom (1967).

In the herbaceous tribe Parianeae, $2n = 44$ has been found for a species of *Pariana* (Calderón & Dressler 2136) (J. Hunziker, 1978, in litt.) and $2n = 22$ for *P. parvispica* (Pohl, 1972), which contrasts with a basic number of $x = 12$ implied in the $2n = 48$ count reported by Reeder et al. (1969) for *P. stenolemma*. In our own cultivated specimens of *Eremitis*, Royce Oliver (pers. comm.) has recently found the two species examined to be high polyploids, with somatic numbers over 60.

In the tribe Streptochaeteae, both species of the single genus, *Streptochaeta*, have been found to be diploids, with $2n = 22$. This count was reported for *S. sodiroana* (Pohl & Davidse, 1971) and *S. spicata* (Valencia, 1962).

We still do not have counts for two of the tribes of herbaceous genera: Anomochloae of South America and Buergersiochloae of New Guinea. We also lack counts for the majority of woody genera.

While the number of chromosomes in the set is important and further counts will be useful in understanding trends of evolution in the subfamily, karyotype analyses should also be undertaken. One such analysis was presented by Daker (1968), who investigated at Kew the cultivated material of the herbaceous bamboo, *Diandrolyra bicolor*. He found only 18 chromosomes in the set and his illustration shows that they are asymmetric. Another such analysis was made by Virkki (1963), who found 18 pairs of metacentric chromosomes in the bamboo, *Swallenochloa* (as *Chusquea*) *subtessellata*. In his study of *Streptochaeta spicata*, Valencia stated that of the eleven pairs of chromosomes he observed at metaphase, the position of the centromere was central in four pairs, while in the others the arms were slightly unequal.

STREPTOCHAETA

A NEW SPECIES

One of the most unusual of the herbaceous bambusoid grasses is the genus *Streptochaeta*, whose remarkable "spikelet" has long been the basis of investigation and speculation. The genus was named by Schrader and published by Nees von Esenbeck, who examined the type specimen in the Berlin herbarium and published the name, *S. spicata*, in 1829. The type specimen came from Felisberto in the state of Bahia, Brazil. In his treatment of the bamboos of that country, Nees (1835) allocated the genera to three groups, one of which included *Streptochaeta* by itself. The following year he made it the basis of a tribe, Streptochaeteae (Nees, 1836).

The genus is found only in tropical America, with the most common species—the type—occurring from southern Mexico to northern Argentina. It is a medium-sized plant with broad, oval leaves generally 2–4.5 cm wide. A less widespread, but not uncommon, species is *S. sodiroana*, which ranges from Guatemala, Honduras, Belize, Costa Rica, and Panama to lowland Ecuador. It is a larger plant

with oval leaves that reach as much as 8 cm across and with smaller but more numerous spikelets in the inflorescence.

Until now, only two species have been known in the genus. However, a third can now be added. In 1972, during a collecting trip through eastern Brazil my colleague, Dimitri Sucre, and I located a population of *Streptochaeta* plants quite distinct from the known species. The genus was immediately recognized by the distinctive spikelets, although they differed from the known ones in size and other features. But the narrow, lanceolate blades presented an especially striking contrast to those of the other two species, which have among the broadest and most ovate blades of any grass. A study of the new species raised again the nature of the so-called "spikelet" in this genus, an interpretation of which I present in the discussion that follows its formal description. I am naming the new species, *Streptochaeta angustifolia*, in obvious reference to its distinctive blades.

Streptochaeta angustifolia Soderstrom, sp. nov. TYPE: Brazil, Espírito Santo, Mun. Cachoeiro de Itapemirim, 10 km from Cachoeiro toward Alegre, 20°47'S, 41°09'W, elev. ca. 90 m, *Soderstrom & Sucre 1969* (RB, holotype; CEPLAC, INPA, K, MO, P, US, isotypes).—FIGS. 5–6.

Gramen perenne, usque ad 70 cm altum. Laminae symmetricae, lanceolatae, 10–15 cm longae, 0.5–1.8 cm latae. Inflorescentia subspicata, 8–11 cm longa, 6–8 spiculis in spiram dispositis. Spiculae 1.0–1.5 cm longae, cum 11 bracteis spiraliter et verticillatim dispositis. Stamina 6, filamentis adnatis; antherae ca. 5.4 mm longae, apicaliter exsertae. Ovarium fusiforme, 3 stigmatibus, ca. 5 mm longis, non-plumosis, apicaliter exsertis.

Perennial with a knotty, short-rhizomatous base of sympodial habit. *Culms* unbranched, erect, hollow with thick walls, 40–70 cm tall, with 4–8 dark, prominent nodes, the internodes 4–14 cm long, in some instances many in succession shortened and resulting in a fascicle of leaves with the sheaths strongly overlapping. *Leaves* evenly distributed along the culm, acuminate at the tip, symmetric at the base, 10–15 cm long, 0.5–1.8 cm wide, scaberulous on the upper surface, glabrous or hirtellous on the lower, the margins entire, the midrib prominent on the upper and lower surfaces, the primary nerves 3 or 4 on each side of the midrib, manifest only on the lower surface, connected by manifest transverse veinlets. Sheaths strongly ribbed, pale green becoming brown, glabrous over the back, ciliate on the upper margins. Petiole lacking, the juncture of blade and sheath a smooth, dark band of tissue covered by cilia abaxially. *Inflorescence* terminating the culm with a second one occasionally produced from a bud in the axil of the uppermost leaf, 8–11 cm long, subspicate with 6–8 "spikelets" arranged spirally on the axis; peduncle 10–13 cm long, pale green, glabrous, becoming flocculose toward the summit, the axis flocculose, exserted well beyond its subtending leaf, the leaf blade sometimes reduced or lacking. *Spikelets* falling entire at maturity, 1.0–1.5 cm long with an awn 3–4 times as long; axis of the spikelet bearing numerous more or less spirally arranged bracts: bracts I–V greenish stramineous, membranous, short, empty, deeply dentate, I and II with 3 or 4 thick nerves, one extending into an awn, 1.3–3.6 mm long, positioned on the side of the spikelet toward the main axis of the inflorescence, near to each other but not overlapping; bracts III–V about the same size and shape, 4–5 mm long, with deeply dentate margins, and with 5 or 6 thick nerves, only slightly overlap-

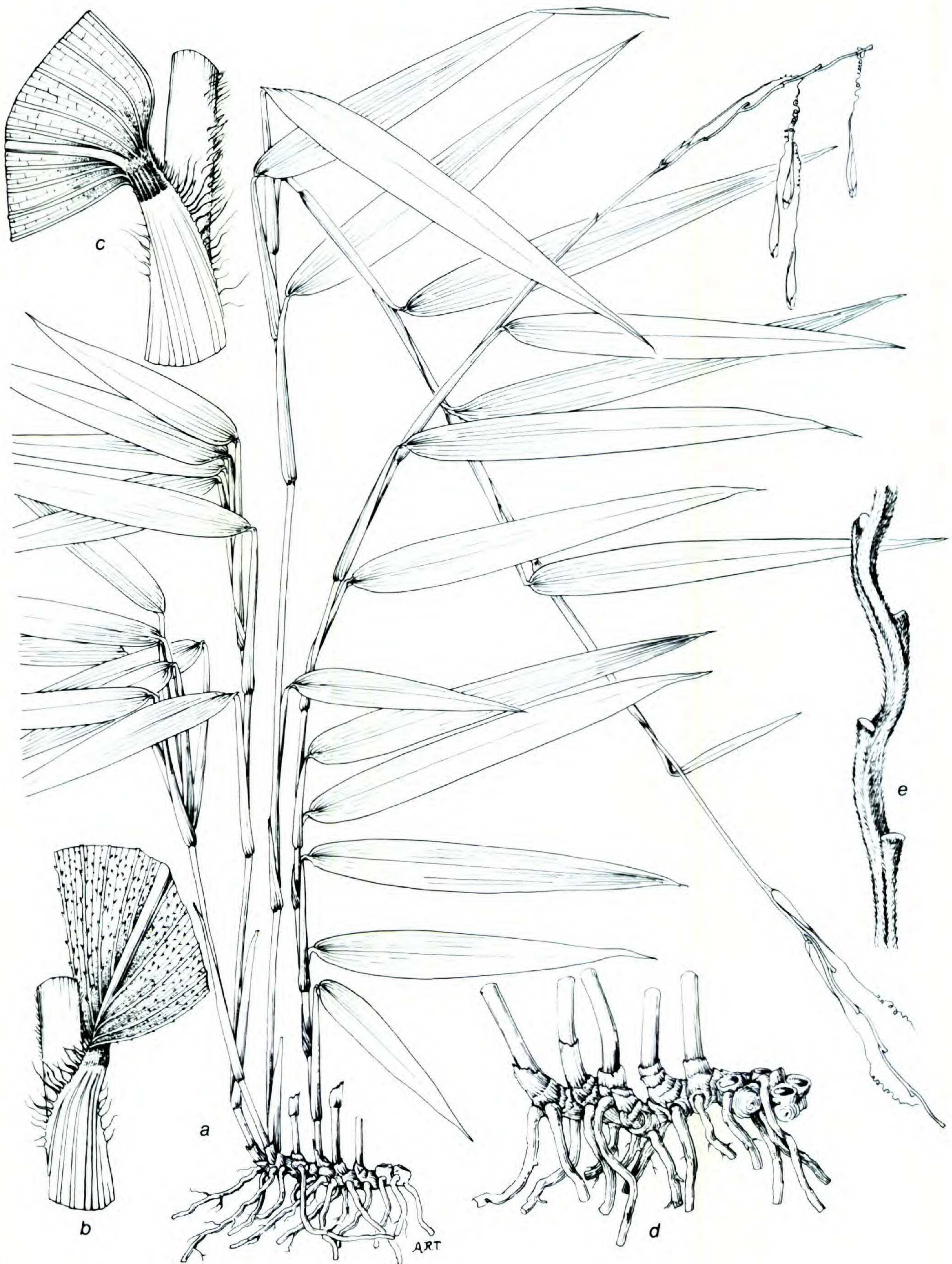


FIGURE 5. *Streptochaeta angustifolia*.—a. Habit ($\times\frac{1}{2}$).—b. Midregion of leaf showing summit of sheath and upper surface of blade ($\times 4.5$).—c. Midregion of leaf showing summit of sheath and lower surface of blade ($\times 5$).—d. Rhizome system with culm base ($\times 1$).—e. Portion of rachis enlarged ($\times 1.5$). [All drawings based on *Soderstrom & Sucre 1969*, Brazil, Espírito Santo, mun. Cachoeiro de Itapemirim.]

ping at the base; bract VI subtending a flowering axis and separated from bracts I–V by a curved glabrous internode, the bract ca. 1–1.4 cm long, elongate, coriaceous, lanceolate, concave, glabrous, 12-nerved, rounded on the back except for a flattened portion at the base from which extends a small, downward-pointing beak, narrowed above and forming a long, slender, tendrillike, coiled awn, 3–5 cm long; bracts VII and VIII lanceolate-triangular, the summits spreading away from each other, 8- or 9-nerved, the bases imbricate, coriaceous, 8.5–10.3 mm long; bract IX lacking; bracts X, XI, and XII a trimerous whorl embracing the androecium and gynoecium, convolute, coriaceous, 12–15-nerved, 12–14.5 mm long. *Stamens* 6, the filaments fused and forming a delicate tube around the gynoecium at anthesis, the anthers yellow, 5.4 mm long, exerted through the apex of the spikelet, the free part of the filaments above ca. 2 mm long, these attached to the anthers about $\frac{1}{4}$ from the base; ovary fusiform, ca. 4 mm long, the style to 3 mm long, the stigmas 3, nonplumose, ca. 5 mm long.

The inflorescence of *Streptochaeta*, including our new species, bears a number of short-pedicellate spikelets on an axis more or less spirally arranged. For *S. spicata*, Arber (1929) reported a $\frac{2}{5}$ phyllotaxy and Page (1951) a $\frac{3}{8}$ phyllotaxy. In that species there are 8–11 spikelets on the axis, in *S. sodiroana* up to 100, and in the new species, 6–8. In all of them the axis terminates in an aborted portion, sometimes represented only by a tuft of hairs.

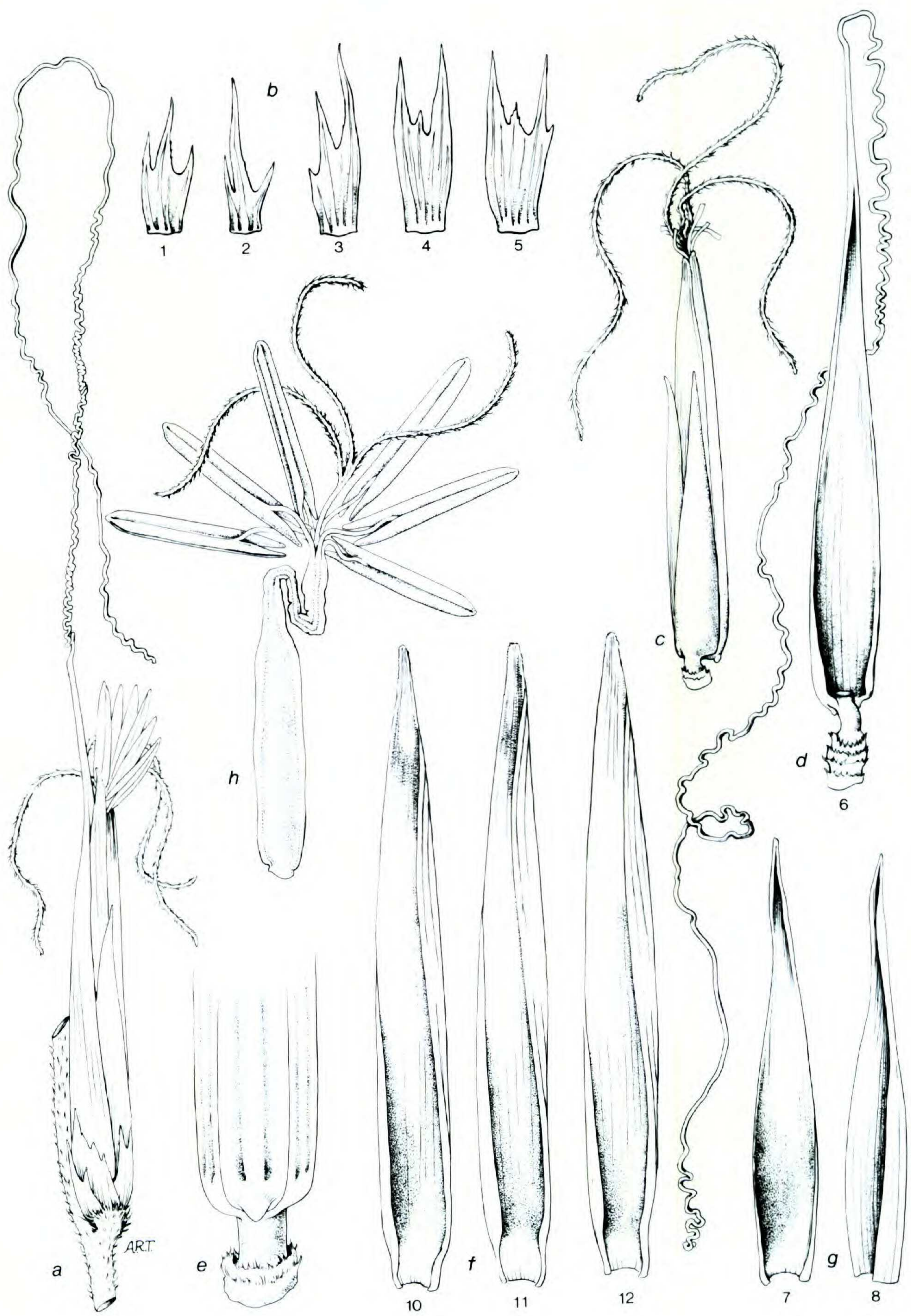
The so-called spikelet (Fig. 6) of *Streptochaeta* is short-pedicellate and bears numerous bracts, again arranged around the axis in a more or less spiral to whorled, but not distichous, fashion. The first two are small and few-nerved, placed side by side, with margins free from one another, and facing the axis; these have thick nerves and are membranous between the nerves. The following three bracts are of the same consistency with thick nerves, deeply dentate margins, but are a little larger than the first two; they are somewhat overlapping at the base. The sixth and succeeding bracts are coriaceous, elongate, many-nerved, and curved. Bract VI bears a long coiled and twisted terminal awn. At maturity the awns of the spikelets become entangled and all the spikelets usually fall or are carried away together.

Above bract VI are two elongate bracts with overlapping bases and narrowed summits that are falcate and point away from each other. Above this pair are three more elongate and coriaceous bracts that form a whorl around the reproductive organs; their margins are overlapping at the base. All of these bracts, the sixth and succeeding ones, form essentially a hard, more or less tubular, structure that surrounds the reproductive organs.

The androecium is composed of six stamens whose filaments are fused at the base. At anthesis the tube elongates and the anthers are thrust out through the top of the spikelet, with the extremely thin, delicate, and transparent tube surrounding the ovary. The anthers are attached to the filaments about one-quarter from the base and do not hang from the spikelet in a versatile manner. The

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FIGURE 6. *Streptochaeta angustifolia*.—a. Pseudospikelet ($\times 4.5$).—b. Series of bracts (1–5) from the base of the pseudospikelet ($\times 6$).—c. Pseudospikelet with basal bracts 1–5 removed and showing bracts 7 and 8, whose bases are overlapping ($\times 4.5$).—d. Bract 6 with long coiled awn ($\times 4.5$).—e. Back portion of the base of bract 6 showing region where embryo exits at germination.—f. Bracts 10–12 ($\times 6$).—g. Bracts 7 and 8 ($\times 6$). Bract 9, which exists in other species, has not been found here.—h.



Ovary with long style and 3 stigmas, surrounded by the thin, fused filaments of the 6 stamens ($\times 4.5$). [All drawings based on *Soderstrom & Sucre 1969*, Brazil, Espírito Santo, Mun. Cachoeiro de Itapemirim.]

gynoecium consists of an elongate ovary, a long style, and three long, nonplumose stigmas that also exit through the summit of the spikelet.

After fertilization the ovary develops into a fruit with a long, linear hilum and small embryo. It is tightly enclosed within the hard bracts, all of which remain together as a unit through germination. At germination the embryo pushes through the noncoriaceous bases of the upper bracts and through a special tissue at the base of bract VI.

ANALYSIS OF *STREPTOCHAETA* SPIKELET

Several important anatomical and morphological studies have been carried out on the genus, the most significant being those of Arber (1929, 1934), Metcalfe (1960), and Page (1947, 1951). The anatomical findings of Page and Metcalfe showed that the leaf is of the bambusoid type, with its complex system of vascular bundles in the keel, the nonradiate chlorenchyma made up of arm cells, and the presence of fusoid cells. The epidermis is also of the bambusoid type, and so is the seedling, as I have shown. Furthermore, the chromosome number of $2n = 22$ corresponds to that of other herbaceous bambusoid grasses of the New World, especially members of the tribes Olyreae and Parianeae. These New World bambusoid grasses, based on numbers derived from $x = 12$, have highly evolved and often specialized inflorescences, a pattern shared by *Streptochaeta*. There is no reason to concur with Butzin (1965), who made this genus the basis of a monotypic subfamily.

The nondistichous arrangement of the spikelets on the inflorescence axis and similar arrangement of the multiple bracts on the spikelet axis have confused botanists since the day the genus was described. The genus has been the subject of investigation by numerous morphologists, and many papers have been published with widely divergent hypotheses concerning the interpretation of the spikelet, among these the works of Doell (1880), Čelakovský (1889), Hackel (1890), Arber (1929), and Page (1951). All authors have agreed that *Streptochaeta* is a primitive grass, perhaps the most so in the family.

Until now interpretations of the spikelet of *Streptochaeta* have been overly influenced, in my opinion, by the nondistichous arrangement of its many parts, in a family where distichy is the rule. Twisting and torsion are prevalent in this taxon, however, and one can see the twisted inflorescence axis with the naked eye. Such a twisting could camouflage a distichous arrangement and bring the parts into a somewhat spiral phyllotaxy. This twisting was probably repeated in the axis of the spikelet, at least historically, and this, with shortening of internodes, could account for some parts appearing to be in whorls. Within the Bambusoideae nondistichous placement of parts is not altogether unusual; as examples, I refer to the glumes of the male spikelets of *Pariana* placed side by side and to the spiral arrangement of spikelet bracts (glumes) in the inflorescence of the bamboo, *Melocanna*, as reported by Petrova (1973). The nonbambusoid grass, *Micraira*, is well known for the spiral arrangement of its leaves.

Page (1951) found that buds would sometimes form in the axils of bracts I–V in *S. spicata*, and Arber (1929) encountered them in some bracts in *S. sodiroana*. While such buds do not normally develop further, even when present, Page found

that in rare instances the bud subtended by bract V would develop partially. In such a case the bract itself elongated, became coriaceous, and produced a coiled awn just like that of bract VI, to which it may thus be considered homologous. Bracts I–VI are therefore homologous structures.

Except for their nondistichous placement on the axis, then, we can consider bracts I–V to be homologous structures that are potentially gemmiferous and are homologous to bract VI, which is long, coriaceous, many-nerved, long-awned and sometimes interpreted as the fertile lemma. It subtends further structures that precede the reproductive organs. These further structures include a pair (sometimes a third developing) with the bases overlapping, sometimes interpreted as two halves of a palea, followed by a whorl of three, universally interpreted as lodicules.

There is no problem in the interpretation of the reproductive organs themselves. The gynoecium bears three, long nonplumose stigmas. Three stigmas are commonly found in bamboos, such as *Arundinaria* and *Bambusa*, and nonplumose stigmas are to be found in such genera as *Eremitis*, *Anomochloa*, *Streptogyna*, and *Pharus*. The androecium consists of six stamens whose filaments are fused at the base and at anthesis extend into a thin, delicate, and translucent tube that surrounds the ovary. Six stamens are of frequent occurrence in the Bambusoideae and are to be found in such genera as *Bambusa* and *Elytrostachys* of the New World and *Melocanna* of the Old. The anthers are thrust through the opening at the top of the spikelet as are the stigmas. They are attached about one-quarter from the base and do not hang in a versatile manner as the anthers of many wind-pollinated grasses. The staminal tube formed by the filaments is extremely thin and fragile, a condition that could only occur in a closed and protected environment, such as that afforded by the whorl of three coriaceous structures that completely envelop and protect it.

The fusion of filaments into a staminal tube occurs throughout the Bambusoideae, and to my knowledge six stamens are always involved. We find this in the herbaceous bambusoid genus, *Froesiochloa*, as well as in all or some species of the following bamboos: *Dendrocalamus*, *Gigantochloa*, *Oxytenanthera*, and *Schizostachyum*. In all of these cases the anthers exit through the apex of the spikelet and the tube is enclosed within hardened scales.

Thus, stamens of *Streptochaeta* are unlike those of most grasses in that the anthers are thrust through the top of the spikelet rather than laterally from it where they can hang in a versatile condition. Whatever the mechanism of pollination may be in this genus, the position of the anthers and the nonplumose nature of the stigmas speak against wind as the agent of pollen transfer, a situation not unknown in the subfamily (Soderstrom & Calderón, 1971).

In most grasses that are wind-pollinated, the bracts (usually lemma and palea) that embrace the reproductive organs spread apart and allow the stamens and stigmas to extend laterally, and after fertilization they again close and protect the developing fruit. The pushing apart of the lemma and palea is brought about by the lodicules which at this moment become swollen and turgid, thus forcing apart these structures. After fertilization they become flaccid and the lemma and palea come together again.

Dobrotvorskaya (1962), who has made extensive studies on lodicules, consid-

ers this to be their primary function. She also feels that they play a role in protecting the ovary and regulating its water metabolism.

In *Streptochaeta* the anthers do not exit laterally, which we can simply observe or deduce from the fused filaments, a condition that would not allow this. The nonplumose stigmas also corroborate the fact that we are not dealing with a wind-pollinated grass in which laterally exiting, versatile anthers are the rule. The primary function of lodicules in *Streptochaeta*, then, does not exist.

In other bambusoid grasses where there is a staminal tube and the anthers exit terminally, there are no lodicules. In all species of *Gigantochloa* the filaments form a tube and lodicules are lacking. I have not found lodicules in *Froesiochloa*; and in those species of *Schizostachyum* that have a staminal tube there are none. In other cases, where the filaments are free but are enclosed in hard scales that do not open and the anthers exit terminally, the lodicules are likewise absent. Such is the case in *Anomochloa* and *Bambusa atra*.

It seems reasonable to assume that *Streptochaeta* has followed the same course of evolution as other bambusoid grasses, and so with the development of the staminal tube and terminal exiting of the anthers there would also be loss of lodicule function and therefore loss of the lodicules themselves. Furthermore, the structures that have been called lodicules are so unlike these organs in any grass, bambusoid or otherwise, that it is difficult to accept them as such. Rather, they may be bracts that are homologous to the "palea bracts," which in turn are homologous to bracts I–VI.

Dobrotvorskaya (1962) presented data from her study of these "lodicules" in *Streptochaeta* that corroborates this hypothesis, even though she did not question their true nature. She referred to the genus as the most primitive grass and accepted the three large scales as lodicules. She pointed out that they protected the delicate staminal tube and resembled bracts to a great degree, not corresponding to usual lodicules, which are small scales. Dobrotvorskaya found that the cells in the lower part of the *Streptochaeta* lodicules reached gigantic size and she compared these to similar cells found in the inner epidermis of the lemma and palea of grasses in the tribe Hordeae. She also observed similar large cells in the lemma and palea of *Anthoxanthum odoratum*, an especially interesting observation, for in that species the ovary is enclosed in a hardened lemma and palea and lodicules are lacking. Thus, the anatomical evidence presented by Dobrotvorskaya favors the interpretation that the lodicules of *Streptochaeta* are bracts homologous to lemmas (or lemma and palea) that protect the ovary, have a water-storage function, and perform a role in the process of floral development.

At this point we should refer to teratological specimens that were studied by Page (1951). She found that in cases where the bud of bract V developed, the bract itself elongated and became similar to bract VI, complete with a long, coiled awn. At the same time the following two bracts, VII and VIII, elongated and produced small, coiled awns, thus indicating an homology between these bracts and all of the preceding ones. Page also presented evidence to show that bracts VII and VIII were on a different axis from bracts I–VI.

A further important point is that in the early stages of development a ridge always develops opposite and above bracts VII and VIII. On rare occasions, in *S. spicata*, Page (1951) found that the ridge developed into a full-grown bract and

completed a whorl of three. Some authors, such as Arber (1929), argued that bracts VII and VIII represented halves of a palea, and the interpretation of these two as members of an outer perianth was the basis of Čelakovský's theory in 1889 that the grass palea originated from two outer perianth parts. Page, however, showed that all three had separate origins, a fact that thus negated these hypotheses.

If the three large bracts that surround the reproductive organs are not lodicules and the two (or three) below them are not halves of a palea, what do they represent? By their size, many-nerved condition, and coriaceous nature, they most resemble bract VI, except for the coiled awn, and I have already pointed out that the "palea bracts" sometimes do, in fact, develop coiled awns that indicate homology with bract VI. I have already suggested that the whorled arrangement of bracts may be brought about by twisting of the axis and shortening of internodes, conditions that appear to be the rule in the inflorescence of this genus.

THE PSEUDOSPIKELET OF BAMBOOS

Two items are especially pertinent to my interpretation of the *Streptochaeta* spikelet: (1) bracts I–V are potentially gemmiferous, and (2) the genus is a member of the Bambusoideae. On the first point rests the assumption that we are not dealing with a spikelet but an inflorescence branch, and on the second the opinion that we should interpret such a branch by analogy to similar structures within related bambusoid grasses.

The numerous, potentially gemmiferous, bracts that we find in the spikelet of *Streptochaeta*, represent a condition that is common in bamboos. Kurz (1876: 262) was, to my knowledge, the first to draw attention to the structure, but it was McClure (1934) who analyzed it in some Chinese species of *Schizostachyum*, and gave further definition to it in later works (1966, 1973). As defined by McClure, a pseudospikelet is a spikeletlike branch of an indeterminately branching inflorescence, and I interpret this to be the condition that we encounter in *Streptochaeta*. I shall henceforth use the term pseudospikelet for the flowering unit in this genus and interpret it by analogy to the pseudospikelet that characterizes many bamboos, rather than to the spikelet that characterizes most other grasses.

As an example of the pseudospikelet, I have illustrated the inflorescence of *Bambusa atra* (Figs. 7a–b), a bamboo native to the Moluccas. As is typical of plants with pseudospikelets, the leaves of the branch, prior to flowering, become progressively smaller until they are represented by sheaths only, each small sheath subtending a bud that may grow into a short flowering axis that is like a spikelet in appearance. While this axis terminates in a spikelet, with bracts (lemmas) that subtend flowers, there are additional bracts below this that subtend prophyllate branch buds instead of being empty like usual glumes. Such a primary pseudospikelet is diagrammed in Fig. 8d. Here the whole axis is subtended by a bract and bears a prophyllum at its first node. A structure comparable to the ordinary spikelet consists of the upper bracts that subtend floral axes (palea and flower) and two empty bracts (glumes) below this series. Below these empty bracts occur several more bracts like the empty ones in all ways except that each subtends a prophyllate bud. This primary pseudospikelet, as shown in Fig. 8c,



FIGURE 7. *Bambusa atra*.—a. Young inflorescence branch ($\times\frac{1}{2}$).—b. Mature inflorescence branch ($\times\frac{1}{2}$).—c. Leaf complement ($\times\frac{1}{2}$).—d. Upper portion of culm leaf from inside to show ligule ($\times\frac{1}{4}$).—e. Upper portion of culm leaf from outside ($\times\frac{1}{4}$).—f. Culm leaf in place ($\times\frac{1}{4}$).—g. Ligule and auricle of foliage leaf ($\times 3$). [All drawings based on fresh material of *Soderstrom & Kulatunge 1600* from plant cultivated at Peradeniya, Ceylon.]

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FIGURE 8. Flowering systems of *Bambusa atra* and *Streptochaeta angustifolia*.—a. Flowering branch of *Bambusa atra*.—b. Schematic diagram of a.—c. Primary pseudospikelet of *Bambusa atra*.—d. Schematic diagram of a primary pseudospikelet such as c.—e. Primary pseudospikelet of



Bambusa atra with secondary pseudospikelets developing in the axils of the basal bracts.—f. Schematic diagram of a primary pseudospikelet with early secondary pseudospikelets, such as e.—g. Mature clusters of pseudospikelets of *Bambusa atra*.—h. Schematic diagram of a fully mature pseudospikelet cluster such as g.—i. Representation of pseudospikelet of *Streptochaeta angustifolia*.—j. Schematic and interpretative diagram of the pseudospikelet in i. [Solid triangle indicates a primary pseudospikelet; open circle with male and female signs indicates fertile floret; solid circle indicates a bud; double-barred flag represents a prophyllum; curved line with hanging tip represents leaf sheath and blade, respectively; curved line alone represents a sheath or subtending bract; broken line represents hypothetical missing structure; wiggly line represents terminal aborted part of axis.]

looks like an ordinary, many-flowered spikelet, but its indeterminate nature becomes apparent upon germination of the lower buds, which themselves develop into flowering axes, or secondary pseudospikelets, as shown in Fig. 8e and diagrammed in Fig. 8f. These secondary pseudospikelets themselves can produce further, tertiary, pseudospikelets, the final result being a cluster of spikelets of various orders, as shown in Fig. 8g and diagrammed in Fig. 8h.

In the case of *Bambusa atra*, which is represented in Fig. 8, the primary pseudospikelets are, of course, the first to develop, but within each spikelet maturation of the florets proceeds acropetally, with the uppermost ones remaining incomplete or aborted.

The number of bracts on a floral axis and the number that are empty or that subtend buds (floral or branch) are variable, as is the quantity of pseudospikelets ultimately produced. In some species (such as *Bambusa glaucescens*) only a few secondary pseudospikelets develop, while in others many are formed in each order and result in a large and dense sphere (as in species of *Dendrocalamus* and *Oxytenanthera*).

Subtending bracts and prophylla in the inflorescence are common in bamboos that bear pseudospikelets. The development of the usual spikelet of determinate growth very likely came about by the loss of subtending bracts, prophylla, and some of the buds. Without much imagination we can derive the spicate inflorescence of *Streptogyna* from a theoretical type like that shown in Fig. 8b by loss of the subtending bracts and in each floral axis loss of the prophyllum, loss of the prophyllate buds in the lower bracts (glumes), and the retention of flowering buds in the upper ones (lemmas). In some cases, such as the bamboo *Chusquea*, four empty bracts generally precede the fertile one (lemma), which subtends a flower. McClure (1973) has referred to these empty bracts as "transitional glumes" to distinguish them from "glumes," which in the ordinary spikelet means the two empty bracts that precede the lemma(s).

The grass panicle can be derived from an elongation of each flowering axis, as shown in Fig. 8h, loss of subtending bracts and prophylla, and of buds from the lower bracts. This would result in determinate spikelets with empty glumes and fertile florets, each pedicellate, and arranged in a panicle, which is common to most grasses.

THE PSEUDOSPIKELET OF *STREPTOCHAETA*

If we regard the flowering unit of *Streptochaeta* as a pseudospikelet and accept the parts as spirally or verticillately arranged due to variations in twisting of the axes and telescoping of the internodes, we can compare it to a fully developed pseudospikelet, as found in *Bambusa atra* (Figs. 7b, 8a-h). Such a comparison allows the following interpretation (cf. Figs. 8i-j):

Bracts I-VI are arranged on the axis (2) of the primary pseudospikelet which aborts at the tip, repeating abortion of the apex of the main inflorescence axis (1). The bract that theoretically would subtend the axis (2) and the prophyllum of this axis have been lost through evolution. The bud subtended by bract VI always germinates and produces a new axis (3), which, theoretically, is the axis of a secondary pseudospikelet. Bract VI is the first of the several coriaceous bracts that surround the reproductive parts and its long, coiled awn later assists

in the dispersal of the fruit that it ultimately harbors. (At this point it is interesting to recall that when the bud subtended by bract V develops, that bract takes on a form and function like bract VI.) Page has given evidence to show that bracts VII and VIII (and therefore IX, which follows) are on an axis separate from bracts X–XII, so I have diagrammed them (Fig. 8j) as on another axis (4), and assumed that the tip of this axis aborted through evolution and that its prophyllum has likewise been lost. Assuming that the branching pattern repeats itself, bract IX theoretically subtends axis (4); this subtending bract sometimes develops. Axis (4), which belongs to the tertiary pseudospikelet, bears three bracts, X–XII, which previous investigators have considered to be lodicules. This axis conceivably could terminate in the flower but if we assume the branching pattern to be consistent throughout, we must assume that the tip of axis (4) aborted in the course of evolution and that bract XII subtends the floral axis. This axis is surrounded and protected by bracts X–XII and the prophyllum (palea) has been lost through evolution as well as the lodicules. The absence of lodicules, androecium of 6 stamens, and gynoecium with 3 stigmas corresponds to the condition we find in *Bambusa atra*, with which we have compared the pseudospikelet of *Streptochaeta*.

When we reexamine bracts I–XII, it becomes apparent that there are three sets of different kinds of bracts. Bracts I–VI are small and scalelike except when subtending a bud that germinates, as is always the case with bract VI and occasionally with bract V. The next set of bracts are VII and VIII, with IX sometimes developed; these two or three are long, coriaceous and many-nerved with falcate tips. Bracts X–XII are also long, coriaceous, many-nerved, and with long, but erect, acute tips. Each set of bracts, similar among themselves but with some differences between each other, pertains to a separate axis: bracts I–VI to the axis of the primary pseudospikelet, VII–IX to that of the secondary pseudospikelet, and X–XII to that of a tertiary pseudospikelet. What has commonly been referred to as the spikelet in *Streptochaeta* is thus a highly modified branching system made up of three orders of pseudospikelets.

Streptochaeta is the only herbaceous bambusoid grass that has retained the pseudospikelet, with the possible exception of *Anomochloa* and the African genera, which I have not yet studied. But like other herbaceous bambusoid grasses its inflorescence has become highly specialized, resulting in a greatly telescoped and modified branching system. I would agree with previous investigators that *Streptochaeta* is among the most primitive of grasses. However, I base this opinion not on its possession of three lodicules and a two-parted palea, structures that I reason are not even present, but on its herbaceous nature and retention of a pseudospikelet.

THE PRIMITIVE BAMBUSOID GRASS

The major natural groups of grasses as we recognize them today (e.g., arundinoid, pooid, oryzoid, bambusoid) doubtless became differentiated early in the evolution of the family and derived from a form adapted for wind pollination. Various extant grasses possess certain features that we presume to be primitive in that they are common to the larger group, monocotyledons, to which grasses belong. We assume that these features, such as three (possibly six) lodicules or

perianth parts, six stamens, and three stigmas, were present in the primitive form that preceded all the major groups.

Chromosome numbers in multiples of six are characteristic of many grasses, including *Oryza* and *Luziola* of the Oryzoideae, *Centosteca* and *Lophatherum* of the centostecoid group, *Arundo* of the Arundinoideae, and many genera of the Bambusoideae. We may postulate that six is indeed the basic number in the subfamily Bambusoideae, although no count of $2n = 12$ has ever been recorded.

To my knowledge, none of the original bambusoid grasses that were diploids of $2n = 12$ now exists. Probably $x = 12$ occurred long ago through doubling and thus brought about this new basic number of polyploid origin. Stebbins (1971: 190–191) pointed out that in “old, mature, or declining polyploid complexes certain segments initiate new series of polyploid numbers in which the basic number that is multiplied is not the original basic number of the complex [in our case, $x = 6$] but some multiple of it [$x = 12$].” These new series are called “secondary cycles of polyploidy.”

At the original tetraploid level of $2n = 24$, there was a period of diversification and differentiation before the higher polyploids appeared. Herbaceous genera such as *Streptogyna*, *Pharus*, *Leptaspis*, and *Puelia* may represent original tetraploids that were adapted to forest conditions. While most such genera have since become extinct, these few—particularly the first three—may have survived because of their adaptation to more disturbed forest conditions than the rest and a more widespread distribution made possible by excellent dispersal mechanisms.

Among the Bambusoideae we consider the above genera, with $2n = 24$, to be diploids, based on the basic number of 12 as opposed to the theoretical basic number of 6. The primitive grass leaf probably had an anatomy most like the present-day pooid type, with a relatively undifferentiated mesophyll and simple epidermis lacking bicellular microhairs. The various modifications that took place in the bambusoid leaf, such as the development of arm cells and fusoid cells, may have been derived from that as an adaptation to the shaded, humid forest conditions which characterize the habitat of the herbaceous bambusoid genera.

Bamboos, whose leaf anatomy and epidermis differ little from those of the herbaceous members, must have evolved from herbaceous ancestors. Bamboos are mostly polyploids, based on $x = 12$, usually tetraploids but in some cases hexaploids. Development of the large woody habit may have been in response to competition with the tree, the major growth form of the forest. The process that led from herbaceous to woody involved an increase in the chromosome number, or polyploidy, development of complex branching at the nodes, an overall increase in size, and emphasis on vegetative growth, such as the development of a strong rhizome system.

This particular stress on vegetative growth with greater longevity of the individual culm and increase in size by branching in the bamboos led, at the same time, to a decrease in flowering. Vegetative reproduction became the dominant condition in bamboos, at the expense of sexual reproduction, which now occurred only at intervals, these sometimes as long as 120 years. With flowering so infrequent, the simultaneous occurrence of this event in two species became too remote a possibility for gene exchange between them to play part in further evolution. By their diminished flowering and the loss of active inflorescence evolution, the bamboos became in essence guardians of ancient flowering systems,

long since lost in all other grasses—including the herbaceous bamboos—that flower every year.

We find such a primitive type of inflorescence in bamboo genera like *Bambusa*, *Dendrocalamus*, and *Oxytenanthera*, where the leaves of a vegetative branch become progressively smaller until they consist only of sheaths that subtend reproductive buds. These buds develop into indeterminate spikeletlike branches called “pseudospikelets.” In the most primitive form, such as in *Bambusa*, the flowers in these pseudospikelets are complete, with three well-developed lodicules, six stamens, and three stigmas. From such a pseudospikelet with complete flowers, we can follow the hypothetical evolution of the usual grass spikelet and its arrangement in a “raceme” or “panicle.” Such a development must have come about by the loss of subtending bracts, prophylla, and buds, which are common in the pseudospikelet, and a decrease in the number of all parts of the flower.

We would predict that in the most primitive herbaceous bambusoid grass the leaves of the axis, as in *Bambusa*, would become progressively smaller until they were reduced to sheaths that subtend pseudospikelets. Except for the lack of subtending bracts, the closest we come to this is *Streptochoeta*, where the pseudospikelet is highly modified. The inflorescence of *Streptogyna* is also primitive in its spicate arrangement, although subtending bracts are not present and the spikelets are of the usual determinate type. In both of these genera, however, the spikelets are bisexual, the former with an unspecialized androecium of six stamens and gynoecium of three stigmas, and the latter with an advanced androecium of three stamens and gynoecium sometimes of two stigmas. The inflorescence of *Anomochloa* may be unspecialized and certainly begs analysis; however, the flower is highly specialized in its lack of lodicules, four stamens, and single nonplumose stigma. The many-flowered, bisexual spikelets of the African genera, *Puelia* and *Guaduella*, which are arranged in panicles, also need further study.

The most highly evolved inflorescences of herbaceous bambusoid grasses are those that are monoecious with one-flowered spikelets. Four tribes exhibit this condition: Buergersiochloaeae, Olyreae, Parianeae, and Phareae. Although Raven & Axelrod (1974: 594) speak of the olyroid grasses as relatively unspecialized, they are, on the contrary, the most specialized in the subfamily. Genera of this tribe have not only reached the monoecious state but within the same plant there is often great differentiation between male and female inflorescences. The tribe, with variable chromosome complements derived from basic numbers lower than 12, appears to be in a state of active evolution. The only herbaceous bambusoid grasses that are diploids based on $x = 12$ are found in the tribes Phareae, Streptogyneae, and Atractocarpeae. All of these tribes are also present in Africa: the first contains *Pharus* of the New World and *Leptaspis* of Africa and Asia; the second contains the genus *Streptogyna* with one species in the New World and one in Africa and Asia; and the third contains two genera—*Guaduella* and *Puelia*—endemic to tropical West Africa. Interestingly, the leaf epidermis of all of these lacks bicellular microhairs, which are commonly found in bambusoid grasses. The seedlings of those studied—*Pharus* and *Streptogyna*—do not have reduced leaves and are the most unspecialized in the subfamily.

We do not, then, have a single most primitive bambusoid grass but rather several, each possessing certain primitive features. The most unspecialized inflo-

rescences of pseudospikelets are found in the polyploid woody genera like *Bambusa*, while the primitive herbaceous growth form occurs in diploid genera like *Streptogyna*. Both of these have chromosome complements based on the primitive basic number of 12.

Streptochaeta, long regarded as the most primitive grass, cannot hold this title alone. It may indeed be regarded as primitive in its herbaceous condition, modified pseudospikelet, and flower that contains six stamens and three stigmas. But its lack of lodicules, nonplumose stigmas, seedlings with reduced leaves, and a chromosome complement based on a derived basic number of $x = 11$, all show advancement.

I do not yet have enough information to postulate the origin of bamboos, but I feel that they have developed from herbaceous stock and have a close and common ancestry. The genera are still not well understood and valid phytogeographical comparisons cannot yet be made. We do know, however, that Africa is poor in bamboos, with few genera and species represented, while Madagascar is the home of several distinct genera. The chromosome numbers of American bamboos tend to be lower while those of Asia are higher, with the greatest concentration of hexaploids occurring in northern Burma and western China.

Clearly we must now study the herbaceous bambusoid grasses of tropical West Africa and the bamboos that occur on Madagascar. An understanding of these may offer further clues regarding the earliest development of the subfamily and aid us in our interpretation of its evolution.

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INDEX TO TAXA

- Anomochloa* Brongniart 18, 35, 36, 41, 43
Anomochloaeae C. E. Hubbard in Hutchinson 17, 18, 29
Anomochlooideae Pilger ex Potzta 15
Anthoxanthum odoratum L. 36
Arberella Soderstrom & Calderón 18
Arundinaria Michaux 16, 18, 27, 35
 gigantea (Walter) Muhlenberg 22, 23, 26
 pygmaea (Miquel) Ascherson & Graebner 16
Arundinoideae Tateoka 42
Arundo L. 42
Atractocarpeae Jacques-Félix ined. 18, 26, 43
Aulonemia aff. *aristulata* (Doell) McClure 21, 22
Bambusa Retzius corr. Schreber 18, 27, 35, 43, 44
Bambusa subgen. *Guadua* (Kunth) Hackel 27, 28
 atra Lindley 36–41
 capitata Trinius 28
 chacoensis Rojas 28
 glaucescens (Willdenow) Siebold ex Holtum 40
 oldhamii Munro 26
 paraguayana (Doell) Bertoni 28
 polymorpha Munro 28
 stenostachya Hackel 26
 tulda Roxburgh 28
Bambuseae Kunth 18
Bambusoideae Nees 15–17, 21, 23, 26, 27, 34, 35, 37, 42
Buergersiochloa Pilger 18
Buergersiochloaeae Blake 18, 29, 43
Bulbulus Swallen 29
Centosteca Desvaux 42
Cephalostachyum 27
 pergracile Munro 28
Chimonobambusa Makino 26, 27
Chusquea Kunth 27, 28, 40
 subtessellata Hitchcock 29
Cryptochloa Swallen in Woodson & Schery 18, 28
 concinna (Hooker f.) Swallen 28
Dendrocalamus Nees 16, 27, 35, 40, 43
 brandisii (Munro) Kurz 28
 giganteus Munro 15, 26, 28
 hamiltonii Nees & Arnott ex Munro 28
 longispathus (Kurz) Kurz 28
 strictus (Roxburgh) Nees 28
Diandrolyra Stapf 18, 22, 23
 bicolor Stapf 29
Ekmanochloa Hitchcock 18
Elytostachys McClure 35
Eremitis Doell in Martius 18, 29, 35
Froesiochloa G. A. Black 18, 35, 36
Gigantochloa Kurz 27, 35, 36
 macrostachya Kurz 28
Guadua Kunth 28
Guaduella Franchet 18, 43
Hordeae Kunth 18, 36
Indocalamus Nakai 26, 27
Leptaspis R. Brown 17, 19, 26, 42, 43
Lithachne Palisot de Beauvois 18, 28
 pauciflora (Swartz) Palisot de Beauvois 21, 22
Lophatherum Brongniart in Duperry 42
Luziola A. L. Jussieu 42
Maclurolyra Calderón & Soderstrom 22
 tecta Calderón & Soderstrom 18, 29
Melocanna Trinius 19, 34, 35
Micraira F. Mueller 34
Micrairoideae Pilger 15
Mniochloa Chase 18
Neurolepis Meisner 26, 27
Ochlandra Thwaites 27, 28
 stridula Thwaites 21, 24
Olyra L. 18
 fasciculata Trinius 26, 28
 latifolia L. 28
 loretensis Mez 23, 24
 micrantha H. B. K. 28
 taquara Swallen 28
Olyreae Kunth 17, 18, 27, 28, 34, 43
Oryza L. 42
Oryzoideae Parodi ined. 42
Oxytenanthera Munro 27, 35, 40, 43
 abyssinica (A. Richard) Munro 26
Panicaceae Kunth 18
Pariana Fusée-Aublet 18, 27, 29, 34
 parvispica Pohl 29
 stenolemma Tutin 29
Parianeae (Hackel) C. E. Hubbard in Hutchinson 17, 18, 29, 34, 43
Phareae Stapf in Thiselton-Dyer 17, 26, 27, 43
Pharus P. Browne 17, 19, 22–24, 26, 35, 42, 43
Phyllostachys Siebold & Zuccarini 27
Piresia Swallen 18, 29
Pooideae 16
Puelia Franchet 18, 19, 26, 27, 42, 43
Raddia A. Bertoloni 18, 23, 24
Raddiella Swallen in Maguire et al. 18, 29
 esenbeckii (Steudel) Calderón & Soderstrom 29
 nana (Doell) Swallen 29
Rehia Fijten 18, 29
 nervata (Swallen) Fijten 29
Reitzia Swallen 18
Sasa Makino & Shibata 27
Schizostachyum Nees 35–37
Shibataea Makino 26, 27
Strephium Schrader ex Nees 18
Streptochoeta Schrader ex Nees 18, 19, 22, 29, 30, 32, 34–41, 43, 44
 angustifolia Soderstrom 30–33, 38, 39
 sodiroana Hackel 29, 32, 34
 spicata Schrader ex Nees 21, 24, 29, 32, 34, 36
Streptochoetaeae Nees in Lindley 17, 18, 29, 44
Streptogyna Palisot de Beauvois 17, 22, 26, 27, 35, 40, 42–44
 americana C. E. Hubbard 24, 25
Streptogyneae C. E. Hubbard ex Calderón & Soderstrom 17, 26, 43
Swallenochloa McClure 27, 28
 subtessellata (Hitchcock) McClure 29
Thamnocalamus Munro 27
Triticum L. 19
Zea L. 19